

Teffichthys wui sp. nov., a new perleidid fish from the Early Triassic of Jiangsu and Anhui, China

XU Guang-Hui¹ YUAN Zhi-Wei² REN Yi^{1,3} LIAO Jun-Ling⁴
ZHAO Li-Jun⁵ SONG Hai-Jun²

(1 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 xuguanghui@ivpp.ac.cn)

(2 State Key Laboratory of Biogeology and Environmental Geology, School of Earth Sciences, China University of Geosciences Wuhan 430074)

(3 University of Chinese Academy of Sciences Beijing 100049)

(4 College of Economics and Trade, Minzu Normal University of Xingyi Xingyi, Guizhou 562400)

(5 Zhejiang Museum of Natural History Hangzhou 310014)

Abstract Perleididae is a group of stem neopterygian fishes known only from the Triassic. Here, we report the discovery of a new perleidid, *Teffichthys wui* sp. nov., based on six well-preserved specimens from the late Smithian (Olenekian, Early Triassic) marine deposits of Jurong, Jiangsu and Chaohu, Anhui, China. This new discovery documents the third and youngest species of *Teffichthys*, which is slightly younger than the Dienerian (Induan) *T. elegans* from Guizhou and the early Smithian *T. madagascariensis* from Madagascar. The new species shows diagnostic features of *Teffichthys* (presence of a spiracular, 38–41 lateral line scales, and no more than three epaxial rays in the caudal fin) but differs from *T. madagascariensis* and *T. elegans* in some autapomorphies (e.g., a horizontal opercle/subopercle contact and smooth scales with a nearly straight posterior margin). The diagnostic features for the genus *Teffichthys* and the family Perleididae are emended based on detailed comparisons of the new taxon with other perleidids. The phylogenetic relationships of perleidids with other stem neopterygians are discussed using a cladistic approach, and the results provide new insights into the phylogeny and classification of main stem neopterygian clades.

Key words Jiangsu, Anhui, Early Triassic, Perleidiformes, osteology, phylogeny

Citation Xu G H, Yuan Z W, Ren Y et al., in press. *Teffichthys wui* sp. nov., a new perleidid fish from the Early Triassic of Jiangsu and Anhui, China. *Vertebrata Palasiatica*. DOI: 10.19615/j.cnki.2096-9899.240528

1 Introduction

Neopterygii is the most taxonomically rich group of ray-finned fishes and is composed of Halecomorphi, Ginglymodi, Teleostei and closely related fossil taxa (Regan, 1923; Schultze, 1966; Patterson, 1973; Gardiner and Schaeffer, 1989; Arratia, 1999; Coates, 1999; Hurley et al., 2007; Cavin, 2010; Grande, 2010; Clarke and Friedman, 2018; Xu, 2021a, b). This

group underwent rapid early radiation in the Early Triassic, with many stem neopterygians and parasemionotid halecomorphs recovered from Spitsbergen, East Greenland, Madagascar, West Canada, the USA, India, Central Siberia and China (Stensiö, 1921, 1932; Nielsen, 1949; Lehman, 1952; Su, 1981; Sytchevskaya, 1999; Xu et al., 2015; Romano et al., 2016, 2017; Marramà et al., 2017; Yuan et al., 2022). Studies of these taxa are important for understanding the early diversification of Neopterygii and the biological recovery in the aftermath of the end-Permian mass extinction (Chen and Benton, 2012; Benton et al., 2013; Dai et al., 2023).

Traditionally, stem neopterygians were referred to the order Subholostei (Brough, 1939; Schaeffer, 1956; Patterson, 1973), or most of them to the order Perleidiformes (Hutchinson, 1973; Bürgin, 1992, 1996; Neuman and Mutter, 2005; López-Arbarello and Zavattieri, 2008; Sun et al., 2008, 2009). Up to 13 families were once assigned to Perleidiformes, and this made the grade notoriously paraphyletic (Yuan et al., 2022). Recent phylogenetic studies constrict the Perleidiformes to include only the family Perleididae, and the classification of stem neopterygians is being reassessed (Xu et al., 2015; Wen et al., 2019; Xu, 2021a, b; Shen and Arratia, 2022; Yuan et al., 2022). The genus *Teffichthys* is a marine stem neopterygian taxon, including two species in the Early Triassic, the type species *T. madagascariensis* from the early Smithian of Madagascar (Lehman 1952; Marramà et al., 2017), and *T. elegans* from the Dienerian (Induan) of Guizhou, China (Yuan et al., 2022). The type species was originally referred to as *Perleidus* (Piveteau, 1934), a genus that now includes two Middle Triassic species, *P. altolepis*, from the Ladinian of Perledo and Monte San Giorgio areas in Italy and Switzerland (Deecke, 1889; Lombardo, 2001), and *P. sinensis* from the Anisian of Luoping, eastern Yunnan in China (Lombardo et al., 2011). Marramà et al. (2017) named *Teffichthys* to accommodate '*Perleidus*' *madagascariensis*, and placed the genus in the subclass Acinopterygii without reference to a particular family or order; however, a recent phylogenetic study (Yuan et al., 2022) supported the placement of *Teffichthys* in the Perleididae (Perleidiformes).

Here, we report the discovery of a new species of *Teffichthys* based on six well-preserved specimens, four from the Lower Qinglong Formation exposed at the Qingshan section in Jurong City, Jiangsu Province and two from the Helongshan Formation at the Majiashan section in Chaohu City, Anhui Province (Fig. 1). Studies of conodont biostratigraphy indicate that the fossil beds in both sections are coeval, with a late Smithian, Olenekian, Early Triassic in age (Liu et al., 2020). In addition to the new species of *Teffichthys*, other bony fishes known from the same fossil beds include a coelacanth, another perleidid (*Plesioperleidus yangtzensis*) and several parasemionotids (Qian et al., 1997; Liu et al., 2002; Jin et al., 2003; Tong et al., 2006). The fish fossils are preserved in calcareous nodules embedded in black shales and mudstones. Taphonomic studies suggest that fish nodules were formed in a calm and euxinic environment with the participation of a vast array of microbes and possibly sulfur-reducing bacteria (Qiu et al., 2019).

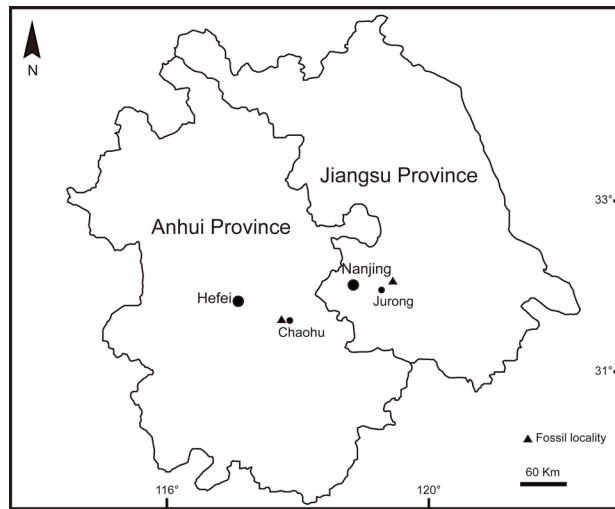


Fig. 1 Map showing fossil localities of *Teffichthys wui* sp. nov.
Map Approval Number: GS(2020)3189

2 Materials and methods

The studied material of the new species of *Teffichthys* includes four specimens stored at the fossil collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) in Beijing, and two specimens (previously referred to *Plesioperleidus jiangsuensis*; Tong et al., 2006) at the YiFu Museum of China University of Geoscience (CUGM) in Wuhan. All specimens were prepared by air-chisels, accompanied occasionally with sharp steel needles. The relative position of fins and scale counts were expressed following Westoll (1944). The traditional actinopterygian nomenclatures (e.g., Gardiner and Schaeffer, 1989; Bürgin, 1992; Xu, 2020a) are generally followed for ease of comparison with most of the existing literatures.

The phylogenetic framework for the discussions provided herein is based on the results of a phylogenetic analysis including 144 morphological characters and 60 actinopterygian taxa (see the electronic supplementary material). The characters were adopted mainly from Xu (2021a) and Yuan et al. (2022). All characters were unordered and equally weighted. The basal actinopterygian *Moythomasia durgaringa* (Gardiner, 1984) was selected as the out-group taxon. The data matrix was generated by WinClada 1.00.08 (Nixon, 2002). Tree searches were accomplished with the heuristic search algorithm (gaps treated as missing data; 1000 random addition sequence replicates; tree bisection-reconnection (TBR) branch-swapping, with 10 trees held at each step and multiple trees saved) in PAUP* 4.0a169 (Swofford, 2003).

Anatomical abbreviations an, anterior nostril; ang, angular; ao, antorbital; apl, anterior pit-line; bf, basal fulcrum; br, branchiostegal ray; cl, cleithrum; den, dentary; dhy, dermohyal; dsp, dermosphenotic; dpt, dermopterotic; es, extrascapular; ff, fringing fulcrum; fr, frontal; gu, gular; io, infraorbital; lgu, lateral gular; mpl, middle pit-line; mx, maxilla; n, nasal; op,

opercle; pa, parietal; pcl, postcleithrum; pf, principle fin ray; pop, preopercle; ppl, posterior pit-line; pra, proximal radial; prr, procurrent ray; pmx, premaxilla; pn, posterior nostril; pt, posttemporal; r, rostral; scl, supracleithrum; scr, sclerotic ring; so, suborbital; sop, subopercle; spi, spiracle; su, supraorbital.

3 Systematic paleontology

Subclass Actinopterygii Cope, 1887

Superdivision Neopterygii Regan, 1923

Order Perleidiformes Berg, 1937

Family Perleididae Brough, 1931

Emended diagnosis A family distinguished from other stem neopterygians by the following unique combination of features: two to five supraorbitals; single suborbital confined between dermosphenotic and preopercle; suborbital half-length of anterior margin of preopercle; opercle no larger than subopercle; preopercle/maxilla contact nearly equal to anterior margin of subopercle in length; supracleithrum slightly deeper than posterior margin of opercle; five or six pairs of branchiostegal rays; no more than seven epaxial rays in caudal fin; no more than 51 lateral line scales.

Content *Perleidus* De Alessandri, 1910; *Meidiichthys* Brough, 1931; *Plesioperleidus* Su et al., 1983; *Plesiofuro* Su, 1993; *Paraperleidus* Zhao & Lu, 2007; *Luopingperleidus* Geng et al., 2012; *Teffichthys* Marramà et al., 2017.

Genus *Teffichthys* Marramà et al., 2017

Emended diagnosis A genus of Perleididae distinguished from other genera of this family by the following features: presence of spiracular; narrow dermosphenotic/preopercle contact; 38–41 lateral line scales; and no more than three epaxial rays in caudal fin.

Teffichthys wui sp. nov.

(Figs. 2–6)

Etymology The specific epithet *wui* is dedicated to Mr. Wu Zi-Hao, who contributed to the fossil collection of the holotype (IVPP V27614).

Holotype IVPP V27614, a relatively complete specimen with part of caudal fin missing, from Qingshan Village, Jurong City, Jiangsu Province.

Referred specimens IVPP V30880, 30881, 30887 from Qingshan, Jurong, Jiangsu; CUGM J2201 and J2202 from Majiashan, Chaohu City, Anhui Province.

Locality and horizon Jurong, Jiangsu, Lower Qinglong Formation; Chaohu, Anhui, Helongshan Formation. Smithian, Olenekian, Early Triassic (Qiu et al., 2019; Liu et al., 2020).

Diagnosis A new species of *Teffichthys* distinguished from other species of this genus by the following features: three supraorbitals; horizontal contact of opercle with subopercle; absence of anterodorsal process of subopercle; 17 dorsal fin rays; smooth scales with nearly straight posterior margin; and pterygial formula of D23/P16, A22–23, C33/T38.

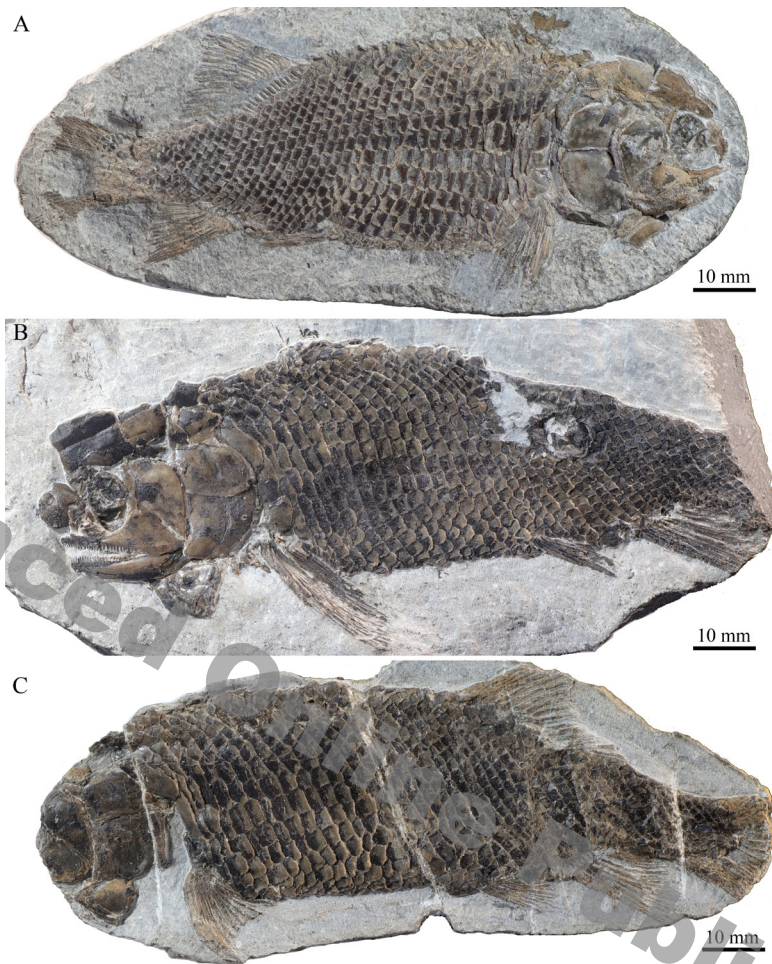


Fig. 2 Specimens of *Teffichthys wui* sp. nov. from Jurong, Jiangsu
A. IVPP V27614, holotype; B. IVPP V30880; C. IVPP V30881

4 Description

General morphology and size Similar to those of other species of *Teffichthys*, *T. wui* has a blunt snout, a fusiform body and an abbreviated heterocercal caudal fin. Among the studied specimens, the holotype (Fig. 2A) is the most complete one, having a standard length (the length from the tip of the snout to the posterior extremity of the caudal peduncle) of 96 mm. The head length (27 mm) is slightly smaller than the greatest body depth (31 mm), which lies midway between the posterior margin of the opercle and the origin of the dorsal fin. The largest known specimen (IVPP V30880) has a length of 108 mm from the tip of the snout to the origin of the ventralmost caudal ray (Fig. 2B). The fragile skeletons are easily broken away during preparation, and the ornamentations of cranial bones are usually poorly-preserved. The endocranium and palatine are unknown because of lateral compression. The caudal fin cannot

be reconstructed because of incomplete preservation, and the vertebral column is not visible due to the squamation *in situ*.

Snout The median rostral is shield-like, being the largest bone of the snout region (Fig. 3D). The depth of the bone is 68% of the length of the frontal. It has a rounded ventral margin, a slightly convex dorsal margin, and curved lateral margins. Each lateral margin of the rostral has a big notch for the anterior nostril. The remaining lateral margin of the rostral sutures with the medial margins of the nasal and the antorbital. The anterior ethmoid commissure of the lateral line system is enclosed in the rostral, indicated by two short canals at the anteroventral portion of this bone (Fig. 3D).

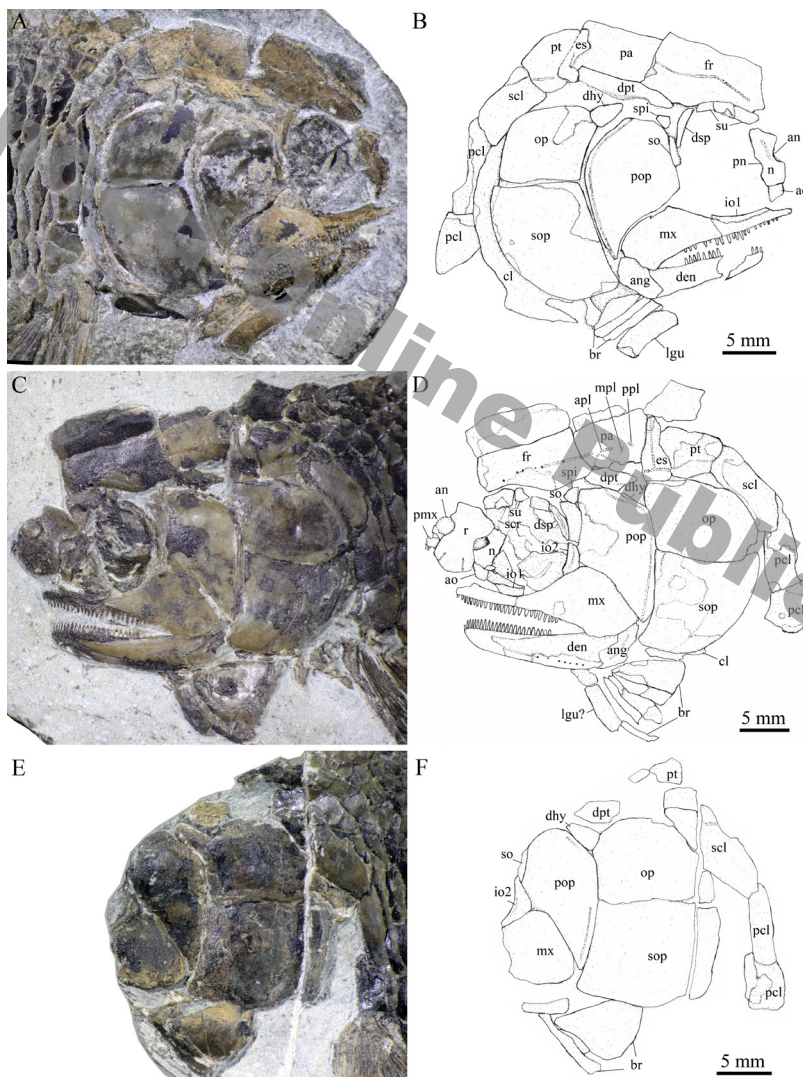


Fig. 3 Photographs (A, C, E) and line-drawings (B, D, F) of skull and pectoral girdle of *Teffichthys wui* sp. nov. from Jurong, Jiangsu
A, B. IVPP V27614; C, D. IVPP V30880; E, F. IVPP V30881

The nasals are relatively large, deeper than wide, with its lateral margin forming the most part of the anterior orbital margin (Fig. 3B, D). The medial margin of the bone is notched for the anterior nostril at its middle portion, and the ventral portion of the lateral margin bears a notch indicating the position of the posterior nostril. An anterior portion of the supraorbital sensory extends anteroventrally at the dorsal portion of the nasal, and ends at the level of the nostril notches (Fig. 3B).

The antorbitals are small and quadrangular, defining the anteroventral margin of the orbit (Fig. 3B, D). The sensory canal is not discernable in the bone because of poor state of preservation.

Skull roof The skull roofing bones include a pair of frontals, parietals, dermopterotics, and extrascapulars (Figs. 3, 4). The frontal is nearly trapezoidal with a relatively narrow portion anterior to the orbital center and a slightly concave posterior margin; it gradually widens posteriorly, reaches its maximal width near the posterior orbital margin, and then becomes slightly narrow posterior to the orbit. The medial suture between frontals is nearly straight.

The parietal is rectangular, longer than wide, being about two-thirds of the frontal length (Figs. 3, 4). Each parietal contacts the frontal anteriorly, the dermopterotic laterally, and the extrascapular posteriorly. The dermopterotic is elongate, about 1.5 times as long as the parietal. It tapers anteriorly and inserts between the frontal and dermosphenotic. The extrascapular is trapezoidal, contacting the parietal and dermopterotic anteriorly. It tapers medially and reaches

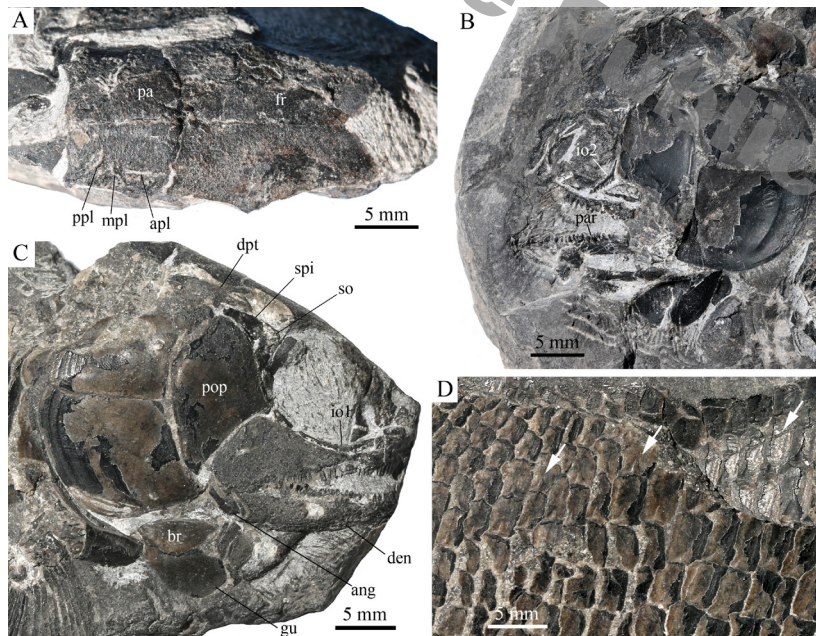


Fig. 4 Skull and scales of *Teffichthys wui* sp. nov. from Chaohu, Anhui

A, C. skull of CUGM J2202 in dorsal (A) and right lateral (C) view; B. skull of CUGM J2201 in left lateral view; D. CUGM J2202, anterior flank scales, with arrows indicating the dorsal peg of the scale

the middle line of the skull.

The supraorbital canal extends longitudinally through the frontal, enters the parietal and ends at the anterior portion of this ossification. Three short pit-lines are discernable in the parietal, including a straight anterior pit-line, a curved, anterolaterally extended middle one, and a posterolaterally extended posterior one (Fig. 4A). The temporal sensory canal extends parallel to the lateral margin of the dermopterotic, and enters the extrascapular posteriorly (Fig. 3D). Additionally, the supratemporal commissure runs transversely through the middle portions of both extrascapulars.

Circumorbital bones There are three supraorbitals flanking the lateral margin of the frontal (Fig. 3B). They are rectangular; the first (anteriormost) is slightly longer than the last one, and the middle one is the shortest (Fig. 3D).

Two infraorbitals are present. The first infraorbital is elongate and tube-like, forming most of the ventral border of the orbit (Fig. 4C). The second is crescent, transferring the infraorbital sensory canal into the dermosphenotic (Figs. 3D, F, 4B).

The dermosphenotic is narrow and deep, forming the posterodorsal margin of the orbit. Posterior to the dermosphenotic, there is a suborbital, which is rectangular, as deep as the dermosphenotic (Figs. 3D, 4C). More posteriorly, an elongate, trapezoidal ossification inserts between the preopercle and dermopterotic. This ossification is labeled as the spiracular (Fig. 4C) following the traditional terminology in *Teffichthys* (Lehman, 1952; Marramà et al., 2017).

Thin sclerotic bones are partly preserved near the orbital rim, but their number and complete shape are still unknown because of incomplete preservation (Fig. 3D).

Jaws The premaxillae are small and poorly preserved. A right premaxilla is partly exposed in IVPP V30880 (Fig. 3D); it is nearly trapezoidal with two conical teeth discernable at its oral margin, and the actual tooth number could be slightly higher (Fig. 5). The maxilla has an elongated infraorbital ramus and a trapezoidal postorbital blade (Figs. 3, 4). The length of the maxilla is 2.5–2.7 times its maximum depth. The posterior margin of the maxilla is rounded, and the tooth-bearing margin is slightly concave. The teeth are distributed only at the infraorbital ramus of the bone. There were 25 peg-like teeth preserved in the maxilla of V30880 (Fig. 3D). The posterior teeth are slightly shorter than the anterior teeth.

The lower jaw is wedge-shaped with two elements, dentary and angular, discernable in lateral view (Figs. 3D, 4C). The supra-angular, commonly present in other stem neopterygians, is not exposed probably because of its small size and the lateral coverage of the maxilla. The dentary is large and stronger than the infraorbital ramus of the maxilla, being 88% of the mandibular length. The oral margin of the dentary is slightly concave, bearing 24 peg-like teeth in V30880 (Fig. 3D). The teeth are nearly equal to those of the maxilla in size. The angular is small and elongate, accounting a quarter of the mandibular length. The mandibular canal extends through the dentary and angular, indicated by a longitudinal canal and a line of small pores parallel to the ventral margin of the dentary, and a curved canal in the angular (Fig. 3D).

The prearticular is plate-like, bearing some blunt, molariform teeth on its oral margin (Fig. 4B).

No other ossifications are discernable from the medial surface of the lower jaw.

Opercular series and dermohyal The opercle and subopercle are trapezoidal, and the contact suture between them is nearly horizontal. The subopercle is approximately 1.5 times as deep as the opercle. It has a straight dorsal margin, lacking an anterodorsal process (Figs. 3, 4). An interopercle is absent, as in other stem neopterygians. The vertically oriented preopercle is deep and quadrangular, with a tapering ventral portion inserting between subopercle and maxilla. The anteroventral margin of the preopercle that contacts the posterodorsal margin of the maxilla is nearly equal to the anterior margin of the subopercle in length. The preopercular sensory canal is indicated by a vertical line of small pores close to the posterior margin of this bone. Additionally, a dermohyal is wedged between the preopercle and opercle. It is small and triangular (Fig. 3).

Branchiostegal rays and gulars A lateral gular and five branchiostegal rays are discernable from the left side of the skull in IVPP V30880 (Fig. 3D). The anterior bone is identified as a lateral gular because it is slightly broader than the anteriormost branchiostegal ray, similar to the condition in *Plesiofuero* (Xu et al., 2015). The lateral gular and anterior four branchiostegal rays are elongate and rectangular, and the posteriormost branchiostegal ray is broad and triangular (Fig. 3). A detached median gular is preserved near the branchiostegal rays; it is heart-shaped, nearly half of the length of the lower jaw (Fig. 4C).

Paired girdles and fins A posttemporal, a supracleithrum, a cleithrum and two postcleithrae are present on each side of the pectoral girdle. The posttemporal is broad and trapezoidal, nearly as wide as the extrascapular. The supracleithrum is rhomboid, slightly deeper than the opercle (Fig. 3D). The lateral line pierces the lateral portion of the posttemporal and extends posteroventrally into the dorsal portion of the supracleithrum.

The cleithrum is large and curved, with the broad orobranchial process anteriorly overlapped by the subopercle (Fig. 3B). There are two postcleithra associated with the cleithrum; the dorsal is rhomboid, as deep as the supracleithrum, and the ventral is trapezoidal.

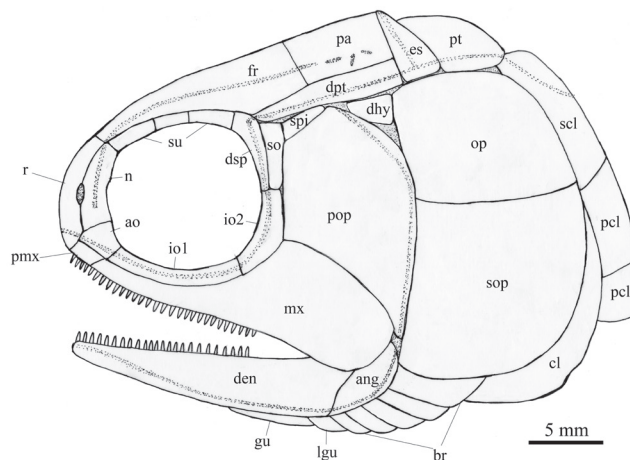


Fig. 5 Reconstruction of skull and pectoral girdle of *Teffichthys wui* sp. nov.

nearly half the depth of the dorsal (Fig. 3).

The pectoral fins are inserted low on the body, and each is composed of 13 distally segmented rays. Except for the first ray, the rays are branched distally. The first ray is relatively short, preceded by one or two basal fulcrum and a series of small, leaf-like fringing fulcra (Fig. 6A). The second ray is the longest, and the remaining rays gradually reduce in length.

The pelvic girdles are not exposed. The pelvic fins are inserted at the 16th vertical scale row, and each is composed of seven distally segmented rays. The first ray is unbranched, preceded by a basal fulcrum and a series of fringing fulcra, and the others are branched distally.

Median fins and pterygiophores The dorsal fin originates above the 23rd vertical scale row. It is composed of 17 distally segmented rays, preceded by three basal fulcra (Fig. 6D). Several small fringing fulcra are discernable, and they are associated with the leading margin of the first unbranched ray; the other rays are branched distally. There are 13 proximal radials below the anterior 13 rays in the holotype; each supports a ray (Fig. 6D). The posterior proximal radials are not exposed.

The anal fin originates below the 22th or 23rd vertical scale row, composed of 12 distally

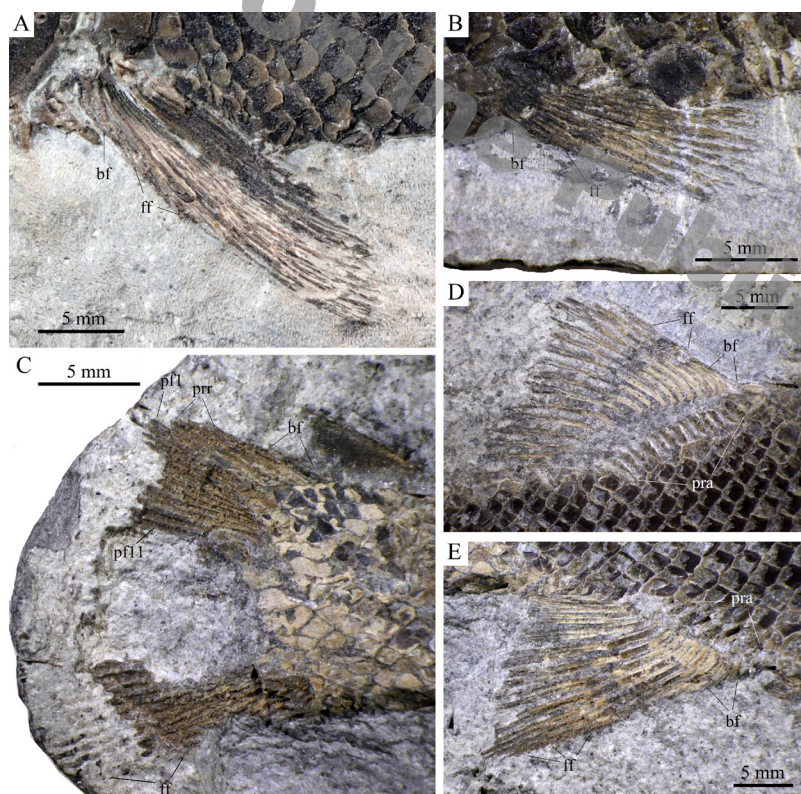


Fig. 6 Fins and scales of *Teffichthys wui* sp. nov. from Jurong, Jiangsu

A. pectoral fin, IVPP V30380; B. anal fin, IVPP V30381;

C, D, E. IVPP V27614: caudal fin (C), dorsal fin (D), and anal fin (E)

segmented rays. The first ray is unbranched, preceded by four basal fulcra and a series of leaf-like fringing fulcra, and the remaining rays are branched distally. The rays are gradually reduced in length posteriorly. Seven proximal radials are exposed, and each supports a ray (Fig. 6E).

The abbreviated heterocercal caudal fin is incompletely preserved, and the total number of rays cannot be counted (Fig. 6C). Three procurent and 11 principal rays can be discernable in the dorsal lobe; among these, four or five are epaxial in position. Some middle rays are missing, and approximately ten principal rays are preserved in the ventral lobe (Fig. 6C). In addition, two epaxial basal fulcra are preserved in the dorsal lobe, and some leaf-like fringing fulcra are associated with the last principal ray.

Scales The body is fully covered with rhomboid scales. The scales are arranged in 38 vertical rows along the main lateral line. In the 13th vertical row of scales, there are 17–19 scales on each side of the body, nine or ten below the lateral line. The lateral line scales and those just below them in the anterior flank region are the largest, nearly twice as deep as long (Fig. 4D). The scales gradually become shorter dorsally, ventrally and posteriorly. They have a nearly smooth outer surface with a straight posterior margin. The peg-and-socket articulation between scales are present as commonly in other early neopterygians (Fig. 4D).

5 Discussion

5.1 Phylogenetic analysis

Our analysis resulted in 468 most parsimonious trees (tree length = 427 steps, consistency index = 0.4496, retention index = 0.7777), a strict consensus of which is presented in Fig. 7. In this cladogram, three orders, Redfieldiiformes, Platysagiiformes and Polzbergiiformes, are nested successively at the basal positions of Neopterygii because they possess the synapomorphies of the total group Neopterygii but lack two uniquely derived features of Colobodontidae and more crownward neopterygians: presence of dorsal and anal fin rays that are segmented only within the distal region, and dorsal and anal fins with a 1:1 ratio of fin rays to endoskeletal radials.

The family Colobodontidae was once considered synonymous with the Perleididae among the Perleidiformes (Stensiö, 1932); however, later studies (Mutter, 2004; Cartanà et al., 2015; Xu, 2020a) revealed that both families are notably different from each other in several aspects: 1) a postrostral is present in the former but is lost in the latter; 2) a suborbital is absent in the former but is present in the latter; 3) the opercle is larger than the subopercle in the former, but the latter shows a reverse condition; 4) the former has a characteristic ornamentation on scales, contrasting the conditions in the latter; and 5) the former has a larger number (56–82) of lateral line scales than does (40–50) in the latter. Furthermore, recent analyses have shown that colobodontids lack several synapomorphies of perleidiforms shared with more derived neopterygians, absence of the dermosphenotic/preopercle contact (reversal in

Pseudobeaconia and *Habroichthys*), six or fewer pairs of branchiostegal rays (reversal in some crown neopterygians), and 24 or fewer principal caudal rays (reversal in *Fuyuanperleidus* and some louwoichthyids). As such, the Colobodontidae is removed from the Perleidiformes and is placed in the new order Colobodontiformes proposed herein (Table 1).

Above the Colobodontiformes, the clade *Plesiofuro*–*Meidiichthys*, *Perleidus*, *Teffichthys* and *Plesioperleidus* form an unresolved polytomy within the Perleididae (Perleidiformes). The perleidids share four synapomorphies: 1) the preopercle/maxilla contact nearly equal to the anterior margin of subopercle in length; 2) the suborbital half as deep as the anterior margin of the preopercle; 3) the opercle no larger than subopercle in size (independently evolved in redfieldiiforms and louwoichthyiforms); and 4) the supracleithrum deeper than the posterior margin of the opercle. Within perleidids, *Teffichthys wui* sp. nov. shares two synapomorphic features with *T. elegans* and *T. madagascariensis*: the presence of a suborbital and a spiracular, and a narrow contact between the preopercle and the dermopterotic. However, the interrelationships between them are unresolved.

More crownward, Louwoichthyiformes, Luganoiiformes, Peltopleuriformes and Venusichthyidae are placed successively at the neopterygian stem (Fig. 7). Louwoichthyiformes and Luganoiiformes are more derived than Perleidiformes because they have a very abbreviated heterocercal caudal fin, and Peltopleuriformes and Venusichthyidae have an almost homocercal caudal fin, resembling many crown neopterygians. In addition, venusichthyids have a high coronoid process, a derived feature previously considered as a synapomorphy of crown neopterygians. Although the Venusichthyidae is sampled here by *Venusichthys comptus* from China only (Xu and Ma, 2016), our comparative study reveals that this family is also known from Europe, represented by some ‘peltopleurids’, e.g., ‘*Placopleurus*’ *besanensis* and ‘*P.*’ *tuberculatus* from the Middle Triassic of Italy and Switzerland (Brough, 1939). Reexaminations on materials of both ‘*Placopleurus*’ species by the first author indicate that they are strikingly different from the type species of the genus *Placopleurus* (*P. primus*; Brough, 1939) but rather resemble *Venusichthys comptus* in many features (e.g., opercular series, jaws and scales). Consequently, we would suggest the reassignment of ‘*P.*’ *besanensis* and ‘*P.*’ *tuberculatus* into the venusichthyid genus *Venusichthys* (Xu and Zhao, 2016).

5.2 Character comparisons

The discovery of *Teffichthys wui* sp. nov. extends the geological range of Chinese *Teffichthys* from the Dienerian (Induan) of Guizhou Province (*T. elegans*; Yuan et al., 2022) into the late Smithian (Olenekian) of Jiangsu and Anhui Provinces. Outside of China, *Teffichthys* is represented only by the type species *T. madagascariensis* from the early Smithian of Madagascar (Lehman 1952; Marramà et al., 2017). *Teffichthys wui* sp. nov. differs from *T. elegans* and *T. madagascariensis* in having a horizontal opercle/subopercle contact, slightly fewer lateral line scales, and a slightly more anteriorly placed dorsal fin with 17 rays. Additionally, the scales of *T. wui* sp. nov. are smooth on the surface, and their posterior margins

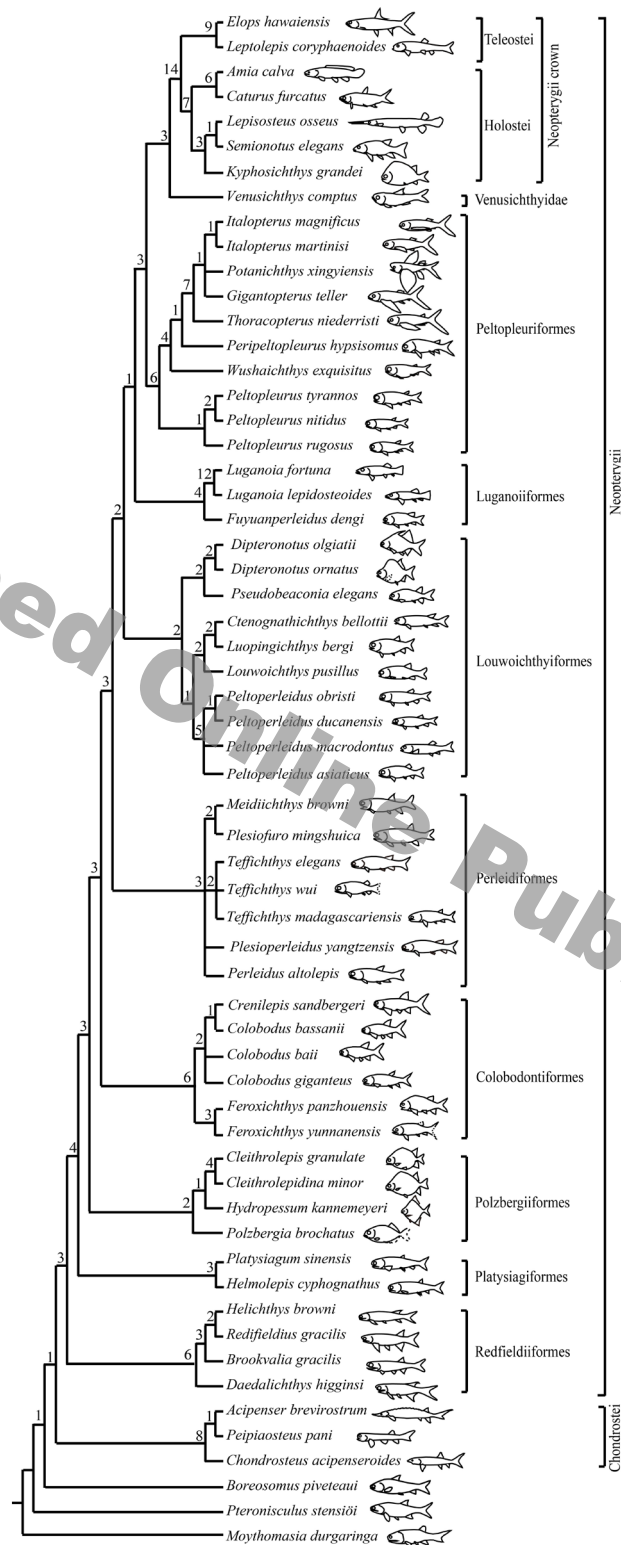


Fig. 7 Strict consensus of 468 most parsimonious trees

Tree length = 427 steps, consistency index = 0.4496, retention index = 0.7777, illustrating the phylogenetic position of *Teffichthys wui* sp. nov. within the Neopterygii. Digits above nodes indicate Bremer decay indices

are nearly straight; in other species of *Teffichthys*, however, the scales have some longitudinal ridges on the outer surface with a serrated posterior margin (Lombardo, 2001; Xu et al., 2015; Marramà et al., 2017; Yuan et al., 2022).

Before our recovery of *Teffichthys wui* sp. nov., Su (1981) and Su and Li (1983) named two perleidid taxa '*Perleidus*' *yangtzensis* and *Plesioperleidus dayeensis* from the Lower Triassic of Anhui and Hubei Provinces, respectively. Later, Qian et al. (1997) and Liu et al. (2002) named additional perleidids, '*Perleidus*' *jiangsuensis*, '*Perleidus*' *eurylepidotrichia* and *Zhangina cylindrica* from the Lower Triassic of Jiangsu Province. Jin et al. (2003) suggested that the latter two perleidids from Jiangsu are synonymous with '*Perleidus*' *jiangsuensis*; the authors agreed on the constriction of *Perleidus* to include only Middle Triassic species (Lombardo, 2001) and referred '*Perleidus*' *jiangsuensis* to the genus *Zhangina*. Tong et al. (2006) and Yuan et al. (2022), however, considered that *Zhangina* is a junior synonym of *Plesioperleidus* according to the law of priority. Our comparative study indicates that

Table 1 Characteristics of main stem neopterygian clades

Order	Family	Characteristics
Redfieldiiformes Berg, 1940	Redfieldiidae Berg, 1940; Brookvaliidae Berg, 1940; Schizurichthyidae Hutchinson, 1973	supraorbital canal reaching dermopterotic; orbit bordered anteriorly by adnasal (supraorbital) and premaxilla-antorbital; one or two pairs of branchiostegal rays
Platysiagiiformes Brough, 1939	Platysiagidae Brough, 1939	nasals joined in midline; absence of suborbital and supraorbital bones; maxilla slender with numerous tiny pointed teeth
Polzbergiiformes Griffith, 1977	Polzbergiidae Griffith, 1977; Cleithrolepididae Wade, 1935; Hydropessidae Hutchinson, 1973	maxilla ending below posterior orbital margin; teeth reduced or lost in both jaws; body deep, with marked dorsal hump; scales deep, ornamented with fine tubercles or rugae
Colobodontiformes ord. nov.	Colobodontidae Andersson, 1916	subopercle with deep anterodorsal process; multiple supraorbitals arranged in more than one horizontal rows; absence of suborbitals; ganoid tubercles on caudal fin rays
Perleidiformes Berg, 1937	Perleididae Brough, 1931	preopercle/maxilla contact nearly equal to anterior margin of subopercle in length; suborbital/preopercle contact nearly half length of anterior margin of preopercle; supracleithrum longer than posterior margin of opercle
Louwoichthyiformes Xu, 2021a	Louwoichthyidae Xu, 2021a; Peltoperleididae Xu, 2021b; Pseudobeacniidae López-Arbarello & Zavattieri, 2008	maxilla relatively short and deep, ending at level of posterior orbital margin; ventral portion of preopercle contacting maxilla anteriorly; subopercle slightly larger than opercle, with prominent anteroventral extension; two or three pairs of branchiostegal rays
Luganoiiformes Lehman, 1958	Luganoiidae Brough, 1939; Fuyuanperleididae Sun et al., 2012	lacrimal fused with maxilla; anterior flank scales greatly deepened, contacting two or three horizontal rows of posterior scales; absence of fringing fulcra
Peltopleuriformes Gardiner, 1967	Peltopleuridae Brough, 1939; Thoracopteridae Griffith, 1977	supraorbital sensory canal ending in the frontal; absence of preopercle/dermopterotic contact; presence of postspiracle; enlarged lateral scutes associated with anal fin; brush-like rays proximally articulating several stout segments at posterior portion of male anal fin
	Venusichthyidae Xu & Zhao, 2016	absence of supraorbitals; oral margin of maxilla convex; two preopercular elements on each side of skull; quadratomandibular articulation below orbital center; two pairs of branchiostegal rays; hook-like contact organ anterior to male anal fin

'*Perleidus*' *jiangsuensis* is a junior synonym of *Plesioperleidus* ('*Perleidus*') *yangtzensis*. *Teffichthys wui* sp. nov. is easily distinguished from *Plesioperleidus yangtzensis* and other *Perleidus*-like taxa in the following aspects:

(1) Relationships between dermopterotic and parietal. *Teffichthys wui* sp. nov. like many other stem neopterygians have a pair of independent parietals (separated from dermopterotics). In contrast, *Plesioperleidus yangtzensis* has a pair of fused parieto-dermopterotics, resembling the conditions of the colobodontid *Feroxichthys* (Xu, 2020a), thoracopterids (Griffith, 1977; Tintori and Sassi, 1992; Xu et al., 2012) and luganoiids (Brough, 1939; Bürgin, 1992; Xu, 2020b).

(2) Supraorbitals. *Teffichthys wui* sp. nov. has three supraorbitals at each side of the skull, consistent with *T. elegans* and *Perleidus altolepis*, but *Plesioperleidus yangtzensis* has only two supraorbitals. Additionally, a little more supraorbitals are present in *T. madagascariensis* (four), *Meidiichthys browni* (four) and *Plesiofuro mingshuica* (five), and numerous supraorbitals in some colobodontids, e.g., nine in *Feroxichthys panzhouensis* and ten or more supraorbitals in *Crenilepis* (Mutter, 2004; Ma et al., 2021). Among stem neopterygians, only a few genera (e.g., *Venusichthys* and *Habroichthys*) lack any supraorbitals (Lin et al., 2011; Xu and Zhao, 2016).

(3) Opercular series. *Teffichthys wui* sp. nov. has an opercle smaller than the subopercle, similar to the conditions in other perleidids and louwoichthyiforms (Lombardo, 2001; Xu et al., 2015; Marramà et al., 2017; Xu, 2021a), and other stem neopterygians generally have an opercle larger than the subopercle. A notable difference within perleidids is that the contact suture between opercle and subopercle is nearly straight and horizontal in *Teffichthys wui* sp. nov., *Perleidus altolepis* and *Plesiofuro mingshuica* but concave and posteriorly inclined in *T. elegans*, *T. madagascariensis* and *Meidiichthys browni* (Hutchinson, 1973; Marramà et al., 2017). The subopercle bears a rudimentary anterodorsal process in *T. elegans* and *Meidiichthys browni*, but this process is absent in *Teffichthys wui* sp. nov. and *Perleidus altolepis* (Lombardo, 2001); additionally, the process is quite deep (44% of the depth of the opercle) in colobodontids (Ma et al., 2021) and many holosteans (Grande and Bemis, 1998).

(4) Lateral line scales and body shape. *Teffichthys wui* has 38 scales along the lateral line, slightly fewer than those in other species of this genus (40 in *T. madagascariensis* and 39–41 in *T. elegans*). In contrast, *Plesioperleidus yangtzensis* has 51 lateral line scales (Qian et al., 1997; Liu et al., 2002; Jin et al., 2003), indicating that its body is more slender than that of *Teffichthys*.

6 Conclusion

The recovery of *Teffichthys wui* sp. nov. documents the third and youngest species of the genus, providing new insights into the morphological diversity and geological range of the perleidids. Detailed comparisons of the new taxon with other perleidids are presented, and the diagnostic features for the genus *Teffichthys* and the family Perleididae are emended

accordingly. The phylogenetic relationships of perleidiforms with other stem neopterygians are discussed using a cladistic approach, and key characteristics of the main stem neopterygian lineages are summarized. The order Perleidiformes is restricted to include only the family Perleididae, and the previously alleged ‘perleidiform’ family, Colobodontidae, is placed in the its own order (Colobodontiformes ord. nov.). The revised topology and systematic classification would be helpful for understanding the sequence of character acquisition in the neopterygian stem.

Acknowledgments We thank Chang M.-M. and Tong J.-N. for constructive suggestions, and Cavin L. and Wu F.-X. for their valuable comments on an earlier version of this manuscript. We also greatly appreciate Niu K.-C., Richter M. and Furrer H. for granting access to comparative fossil materials in Yingliang Stone Natural History Museum (Nan’an), Natural History Museum (London) and Paläontologisches Institut und Museum, Universität Zürich (Zürich), respectively.

Supplementary materials can be found on the website of Vertebrate Palasiatica (<http://www.vertpala.ac.cn/CN/10.19615/j.cnki.2096-9899.240528>).

江苏安徽早三叠世裂齿鱼科一新种：吴氏三叠鱼

徐光辉¹ 袁志伟² 任 艺^{1,3} 廖浚伶⁴ 赵丽君⁵ 宋海军²

(1 中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(2 中国地质大学地球科学学院, 生物地质与环境地质国家重点实验室 武汉 430074)

(3 中国科学院大学 北京 100049)

(4 兴义民族师范学院经济贸易学院 贵州兴义 562400)

(5 浙江自然博物院 杭州 310014)

摘要：裂齿鱼科是新鳍鱼类干群的一支，只生活于三叠纪。根据江苏句容和安徽巢湖早三叠世奥伦尼克期晚史密斯亚期海相地层中发现的6块保存较好的化石，命名了裂齿鱼科一新种，吴氏三叠鱼(*Teffichthys wui* sp. nov.)。它代表了三叠鱼属的第三个种，时代上略晚于非洲马达加斯加早史密斯亚期的马达加斯加三叠鱼和贵州印度期晚第纳尔亚期的优雅三叠鱼，是该属迄今已知最年轻的种。新种具有三叠鱼属的共近裔特征(一块喷水骨，38–41列侧线鳞，尾鳍轴上鳍条不超过3条)，但同时它以一些自近裔特征与马达加斯加三叠鱼和优雅三叠鱼相区别，如主鳃盖骨和下鳃盖骨水平接触，鳞片光滑并且后缘无锯齿。根据新种与其他裂齿鱼科鱼类的详细比较，修订了三叠鱼属及裂齿鱼科的鉴定特征。在分支系统学研究的基础上，讨论了裂齿鱼科与其他新鳍鱼类干群的系统发育关系。研究结果为了解新鳍鱼类干群的系统发育和分类提供了新的信息。

关键词：江苏，安徽，早三叠世，裂齿鱼目，骨骼学，系统发育

References

- Arratia G, 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: Arratia G, Schultze H P eds. Mesozoic Fishes 2 – Systematics and Fossil Record. München: Verlag Dr. F. Pfeil. 265–334
- Benton M J, Zhang Q Y, Hu S X et al., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth Sci Rev*, 125: 199–243
- Berg L S, 1937. A classification of fish-like vertebrates. *Bull Acad Sci l'URSS*, 4: 1277–1280
- Brough J, 1931. The Triassic fishes of the Karroo System and some general considerations on the bony fishes of the Triassic period. *Proc Zool Soc London*, 1931: 235–296
- Brough J, 1939. The Triassic Fishes of Besano, Lombardy. London: British Museum (Natural History). 1–117
- Bürgin T, 1992. Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). *Schweiz Paläont Abh*, 114: 1–164
- Bürgin T, 1996. Diversity in the feeding apparatus of perleidid fishes (Actinopterygii) from the Middle Triassic of Monte San Giorgio (Switzerland) In: Arratia G, Viohl G eds. Mesozoic Fishes and Paleoeology. München: Verlag Dr. F. Pfeil. 555–565
- Cartanyà J, Fortuny J, Bolet A et al., 2015. *Colobodus giganteus* (Beltan, 1972) comb. nov. from the Upper Muschelkalk facies of Catalonia (NE Iberian Peninsula). *Neues Jahrb Geol Paläont Abh*, 278: 323–333
- Cavin L, 2010. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften*, 97: 1035–1040
- Chen Z Q, Benton M J, 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat Geosci*, 5: 375–383
- Clarke J T, Friedman M, 2018. Body-shape diversity in Triassic–Early Cretaceous neopterygian fishes: sustained holostean disparity and predominantly gradual increases in teleost phenotypic variety. *Paleobiology*, 44: 402–433
- Coates M I, 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. *Philos Trans R Soc Lond B*, 354: 435–462
- Cope E D, 1887. Zittel's manual of palaeontology. *Am Nat*, 21: 1014–1019
- Dai X, Davies J, Yuan Z W et al., 2023. A Mesozoic fossil lagerstätte from 250.8 million years ago shows a modern-type marine ecosystem. *Science*, 379: 567–572
- De Alessandri G, 1910. Studii sui pesci triasici della Lombardia. *Mem Soc Ital Sci Nat*, 7: 1–147
- Deecke W, 1889. Ueber Fische aus verschiedenen Horizonten der Trias. *Palaeontographica*, 35: 97–138
- Gardiner B G, 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bull Br Mus Nat Hist Geol*, 37: 173–428
- Gardiner BG, Schaeffer B, 1989. Interrelationships of lower actinopterygian fishes. *Zool J Linn Soc*, 97: 135–187
- Geng B H, Jin F, Wu F X et al., 2012. New perleidid fishes from the Middle Triassic strata of Yunnan Province. *Geol Bull China*, 31: 915–927
- Grande L, 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Amer Soc Herp Spec Pub*, 6: 1–871
- Grande L, Bemis W E, 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal

- anatomy: An empirical search for interconnected patterns of natural history. *Mem Soc Vert Paleont*, 4: 1–690
- Griffith J, 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zool J Linn Soc*, 60: 1–93
- Hurley I A, Mueller R L, Dunn K A et al., 2007. A new time-scale for ray-finned fish evolution. *Proc R Soc B*, 274: 489–498
- Hutchinson P, 1973. A revision of the redfieldiiform and perleidiiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bull Br Mus Nat Hist (Geol)*, 22: 235–354
- Jin F, Wang N Z, Cai Z Q, 2003. A revision of the perleidiid fishes from the Lower Yangtze region of south China - Second report on the fish sequence study near the Permian-Triassic boundary in south China. *Vert Palasiat*, 41: 169–184
- Lehman J P, 1952. Étude complémentaire des poissons de l'Eotrias de Madagascar. *Kungl Svenska Vetenska Handl Ser 4*, 2: 1–201
- Lin H Q, Sun Z Y, Tintori A et al., 2011. A new species of *Habroichthys* Brough, 1939 (Actinopterygii; Peltopleuriformes) from the Pelsonian (Anisian, Middle Triassic) of Yunnan Province, South China. *Neues Jahrb Geol Paläont Abh*, 262: 79–89
- Liu G B, Feng H Z, Wang J X et al., 2002. Early Triassic fishes from Jurong, Jiangsu. *Acta Palaeont Sin*, 41(1): 27–52
- Liu S, Sun Z Y, Ji C et al., 2020. Conodont biostratigraphy and age of the Early Triassic fish-bearing-nodule levels from Nanjing and Jurong, Jiangsu Province, South China. *J Earth Sci*, 31: 9–22
- Lombardo C, 2001. Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): anatomical descriptions and nomenclatural problems. *Riv Ital Paleont Stratigr*, 107: 345–369
- Lombardo C, Sun Z Y, Tintori A et al., 2011. A new species of the genus *Perleidus* (Actinopterygii: Perleidiformes) from the Middle Triassic of southern China. *B Soc Paleontol Ital*, 50: 75–83
- López-Arbarello A, Zavattieri A M, 2008. Systematic revision of *Pseudobeaconia* Bordas, 1944, and *Mendocinichthys* Whitley, 1953 (Actinopterygii: 'Perleidiformes') from the Triassic of Argentina. *Palaeontology*, 51: 1025–1052
- Ma X Y, Xu G H, Geng B H, 2021. *Feroxichthys panzhouensis* sp. nov., a hump-backed colobodontid (Neopterygii, Actinopterygii) from the early Middle Triassic of Panzhou, Guizhou, China. *PeerJ*, 9: e11257
- Marramà G, Lombardo C, Tintori A et al., 2017. Redescription of '*Perleidus*' (Osteichthyes, Actinopterygii) from the Early Triassic of northwestern Madagascar. *Riv Ital Paleont Stratigr*, 123: 219–242
- Mutter R I, 2004. The "perleidiiform" family colobodontidae: a review. In: Arratia G, Tintori A eds. *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*. München: Verlag Dr. F. Pfeil. 197–208
- Neuman A G, Mutter R J, 2005. *Helmolepis cyphognathus*, sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). *Can J Earth Sci*, 42: 25–36
- Nielsen E, 1949. Studies on Triassic fishes from East Greenland. II. *Australosomus* and *Birgeria*. *Medd Grønland*, 146: 1–309
- Nixon K C, 2002. WinClada, version 1.00.08. Available at <http://www.cladistics.com>.
- Patterson C, 1973. Interrelationships of holosteans. In: Greenwood P H, Miles R S, Patterson C eds. *Interrelationships of Fishes*. London: Academic Press. 233–305
- Piveteau J, 1934. Paléontologie de Madagascar XXI. Les poissons du Trias inférieur. Contribution à l'étude des actinopterygiens. *Ann Paléontol*, 23: 81–180
- Qian M P, Zhu S P, Zhao F M et al., 1997. Discovery of Early Triassic fish fossils and its significances in Jourong, Jiangsu

- Province. *Jiangsu Geol*, 21: 65–71
- Qiu X C, Xua Y L, Chen Z Q et al., The Early Triassic Jurong fish fauna, South China: age, anatomy, taphonomy, and global correlation. *Glob Plan Chan*, 180: 33–50
- Regan C T, 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proc Zool Soc Lond*, 1923: 445–461
- Romano C, Koot M B, Kogan I et al., 2016. Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biol Rev*, 91: 106–147
- Romano C, Jenks J F, Jattiot R et al., 2017. Marine Early Triassic Actinopterygii from Elko County (Nevada, USA): implications for the Smithian equatorial vertebrate eclipse. *J Paleontol*, 91: 1025–1046
- Schaeffer B, 1956. Evolution in the Subholostean Fishes. *Evolution*, 10: 201–212
- Schultze H P, 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid zu Rundschuppen). *Neues Jahrb Geol Paläont Abh*, 126: 232–314
- Shen C C, Arratia Gloria, 2022. Re-description of the sexually dimorphic peltopleuriform fish *Wushaichthys exquisitus* (Middle Triassic, China): taxonomic implications and phylogenetic relationships. *J Syst Palaeont*, 19: 1317–1342
- Stensiö E A, 1921. Triassic fishes from Spitzbergen. II. *Kungl Svenska Vetenska Handl*, 3: 1–261
- Stensiö E A, 1932. Triassic fishes from East Greenland. *Medd Grønland*, 83: 1–305
- Su D Z, 1981. A new species of *Perleidus* from Hanui. *Vert PalAsiat*, 19: 107–112
- Su D Z, 1993. New Jurassic ganoid fishes from northwestern Gansu, China. *Vert PalAsiat*, 31: 1–14
- Su D Z, Li Z C, 1983. A new Triassic perleidid fish from Hubei, China. *Vert PalAsiat*, 21: 9–17
- Sun Z Y, Tintori A, Lombardo C et al., 2008. A new species of the genus *Colobodus* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. *Riv Ital Paleont Stratigr*, 114: 363–376
- Sun Z Y, Tintori A, Jiang D Y et al., 2009. A new perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geol Sin*, 83: 460–470
- Swofford D L, 2003. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts
- Sytchevskaya E K, 1999. Freshwater fish fauna from the Triassic of Northern Asia. In: Arratia G, Schultze H P eds. *Mesozoic Fishes 2 – Systematics and Fossil Record*. München: Verlag Dr. F. Pfeil. 445–468
- Tintori A, Sassi D, 1992. *Thoracopterus* Bronn (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. *J Vert Paleontol*, 12: 265–283
- Tong J N, Zhou X G, Erwin D H et al., 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. *J Paleontol*, 80: 146–161
- Wen W, Hu S X, Zhang Q Y et al., 2019. A new species of *Platysiaugum* from the Luoping Biota (Anisian, Middle Triassic, Yunnan, South China) reveals the relationship between Platysiagidae and Neopterygii. *Geol Mag*, 156: 669–682
- Westoll T S, 1944. The Haplolepididae, a new family of Late Carboniferous bony fishes – A study in taxonomy and evolution. *Bull Am Mus Nat Hist*, 83: 1–121
- Xu G H, 2020a. *Feroxichthys yunnanensis* gen. et sp. nov. (Colobodontidae, Neopterygii), a large durophagous predator

- from the Middle Triassic (Anisian) Luoping Biota, eastern Yunnan, China. PeerJ, 8: e10229
- Xu G H, 2020b. A new species of *Luganoia* (Luganoiidae, Neopterygii) from the Middle Triassic Xingyi Biota, Guizhou, China. Vert PalAsiat, 59: 169–199
- Xu G H, 2021a. A new stem-neopterygian fish from the Middle Triassic (Anisian) of Yunnan, China, with a reassessment of the relationships of early neopterygian clades. Zool J Linn Soc, 191: 375–394
- Xu G H, 2021b. The oldest species of *Peltoperleidus* (Louvoichthyiformes, Neopterygii) from the Middle Triassic (Anisian) of China, with phylogenetic and biogeographic implications. PeerJ, 9: e12225
- Xu G H, Ma X Y, 2016. A Middle Triassic stem-neopterygian fish from China sheds new light on the peltopleuriform phylogeny and internal fertilization. Sci Bull, 61: 1766–1774
- Xu G H, Zhao L J, 2016. A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics. Sci Bull, 61: 338–344
- Xu G H, Zhao L J, Gao K Q et al., 2012. A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates. Proc R Soc B, 280: 20122261
- Xu G H, Gao K Q, Coates M I, 2015. Taxonomic revision of *Plesiofuro mingshuica* from the Lower Triassic of northern Gansu, China, and the relationships of early neopterygian clades. J Vert Paleontol, 35: e1001515
- Yuan Z W, Xu G H, Dai X et al., 2022. A new perleidid neopterygian fish from the Early Triassic (Dienerian, Induan) of South China, with a reassessment of the relationships of Perleidiformes. PeerJ, 10: e13448
- Zhao L J, Lu L W, 2007. A new genus of Early Triassic perleidid fish from Changxing, Zhejiang, China. Acta Palaeontol Sin 46: 238–243